

11. ARE THERE ASSEMBLY RULES FOR SUCCESSIONAL COMMUNITIES?

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INTRODUCTION

'Assembly' is putting together a number of parts to make something; 'rules' imply that the process is not random. Probably the first, and certainly the best known use of the term 'assembly rule' for ecological communities was by Diamond (1975). Diamond highlighted interspecific competition for resources as the major factor underlying rules of assembly in sets of New Guinea birds; but it is easy to imagine other forms of interspecific or species-environment interactions as part of the rules, particularly in successional systems (McIntosh 1980). Odum (1969) had no doubt that succession was governed by rules. He wrote (p. 262): Succession 'is an orderly process of community development that is reasonably directional and, therefore, predictable. It results from modification of the physical environment by the community; that is, succession is community-controlled.'

If there are assembly rules for successional communities, what are they, and how well do we understand them? This chapter tries to provide answers, starting with assembly rules for plant populations during succession, before moving up one or more trophic levels to consider animals. I then add complexity by looking at the effects of plant succession on animals, and the impact of animals (herbivores) on plant succession. There follow brief remarks about plant pathogens and more extensive speculations on the role of mutualists. Finally, individual 'pair-wise' interactions are subsumed into community-wide webs of interactions. I have basically taken the view that assembly rules arise from species interactions. Table 11.1 summarizes the 'pair-wise' processes dealt with, however briefly, in the text. I think it is probably impossible, given the relatively primitive state of current knowledge, to rank these processes according to their importance in community assembly.

I have restricted the scope of the review almost entirely to terrestrial ecosystems, and to successions based on green plants. Succession in freshwater and marine habitats, and heterotrophic successions in dung, dead wood, detritus and corpses are wilfully ignored.

TABLE 11.1. Summary of the 'pair-wise' interactions dealt with in the chapter that might, or are known to, contribute to assembly rules for successional communities. The blank cells are fairly easily filled in, although they are not explicitly discussed here; for example, consider the role of carnivores in regulating herbivore populations, with potentially important effects on succession via the herbivores. The entire web of community interactions, both direct and indirect, may potentially influence succession

	Plants	Herbivores	Carnivores	Mutualists	Pathogens
Plants	Effects of plants on plants: Interspecific competition Facilitation Inhibition Tolerance Allelopathy	Effects of herbivores on plants: Herbivory modifies succession		Effects of mutualists on plants: Mycorrhiza N-fixing organisms Pollinators Seed dispersers Ant-extrafloral nectary interactions	Effects of pathogens on plants: Diseases may modify succession
Herbivores	Effects of plants on animals: Animal populations wax and wane along successional gradients created by plants.	Effect of herbivores on herbivores: Interspecific competition in changing environments may drive some species turnover	Effect of carnivores on herbivores: Not discussed but by regulating herbivore populations, the potential effect of carnivores is clearly important	Effect of mutualists on herbivores: Ants attending herbivorous insects	
Carnivores	Animals respond 'passively' to changing habitats created by plant succession		Effect of carnivores on carnivores: Interspecific competition in changing environments may drive some species turnover		

ASSEMBLY RULES FOR VEGETATION

The quintessence of terrestrial succession is a change in the species composition and structure of vegetation. Studies on these phenomena have a long pedigree in ecology, inspiring classical work by F.E. Clements, H.C. Cowles, H.A. Gleason, Sir Arthur Tansley, and A.S. Watt to name but a few. Jackson (1981) provides an introduction to this early literature, drawing attention to approximately 100 papers published in *Journal of Ecology*, *Journal of Animal Ecology*, *Ecology* and *American Naturalist* between 1919 and 1959 that deal in one way or another with the role of competition between plant species as a driving force in succession. Jackson notes (p. 893): 'Much of what is considered original to modern niche theory of competition, except the mathematics, was well formulated and understood by many plant ecologists, especially in England as early as 1914.' This body of work makes plain that interspecific competition, Diamond's *raison d'être* for assembly rules, is a major ingredient in the assembly of successional plant communities. (See McIntosh 1980, and Grime, Chapter 20, for further discussions).

Obviously, however, interspecific competition is not the only cause of vegetation change, a fact that has again been known for a long time (McIntosh 1980). As early as 1916, for example, Clements recognized the importance of chance colonization, as well as habitat alteration and interspecific competition in plant succession (Clements 1916; MacMahon 1981). Contemporary understanding of the processes determining patterns of succession in vegetation (i.e. processes involving only the plants) can be gathered under four headings (there are other ways of classifying the problem, involving greater subdivision of processes, but these four will do) (Connell & Slatyer 1977; Golley 1977; McIntosh 1980; Schowalter 1981; Horn 1981; Hils & Vankat 1982; Crawley 1983; Finegan 1984; Krebs 1985). Each model specifies a particular set of rules (or lack of them) for community assembly during succession:

The facilitation model. Species occurring early in succession modify the habitat, making it less suitable for themselves and more suitable for later colonists.

The inhibition model. Whichever plant species reaches a site first, holds it against all subsequent invaders until it dies.

The tolerance model. Slower growing, more tolerant (competitively superior) plant species invade and mature in the presence of earlier, faster growing, but less tolerant species, and eventually exclude them.

The random colonization model. Succession involves no more than chance survival of different species at the time succession is initiated, and subsequent random colonization by new species; species then grow and

mature at different rates. There is no facilitation, nor are interspecific interactions important.

Except insofar as species differ in dispersal abilities, the fourth and last possibility comes nearest to a 'no assembly rule' model of succession. All the other possibilities constitute assembly rules. Uncertainty therefore lies not with formulating what the rules might be, but with their relative contributions in different habitats and biomes, or along primary and secondary successions. There is also disagreement about the importance of particular means of facilitation or inhibition, for example on the role of allelopathy (see Golley 1977, and Harper 1977 for discussions). Several recent reviews come to markedly different conclusions about the relative importance of the four models (Connell & Slatyer 1977; MacMahon 1981; Finegan 1984; Krebs 1985), with no clear consensus about how succession works (McIntosh 1980; Crawley 1983). Hils & Vankat (1982) modestly conclude that more than one mechanism probably operates at the same time, even in the same abandoned old-field. In other words, as is so often the case in ecology, we must seek a multiplicity of explanations. There is not one universal truth.

For plant succession, possible assembly rules, embodied in the four models, are well defined; relative roles are much harder, and will take much longer, to work out.

CHANGES IN ANIMAL SPECIES ALONG SUCCESSIONAL GRADIENTS

Interspecific competition or habitat selection?

It is hardly surprising that as plant communities wax and wane, so do associated animals, influenced by changing microclimates, food supplies, hiding places, resting sites and so on (e.g. Lowrie 1948; Lack & Lack 1951; Yapp 1962; Shelford 1963; Chevin 1966; Karr 1968; Lack 1971; Healey 1972; Glowaciński & Järvinen 1975; MacMahon 1981; Fuller 1982; Price 1984).

Diamond (1975) clearly recognizes that particular habitat preferences by different species result in bird communities that are not random samples drawn from a pool of all potential colonists. Such individual habitat preferences constitute simple assembly rules, applicable to successional systems or indeed to any type of community. However, as we have already noted, Diamond argues that individual habitat selection alone is insufficient to account for the structure of New Guinea bird communities. The missing ingredient, he suggests, is interspecific competition, excluding species from otherwise suitable habitats.

This important question has triggered a large, confusing and at times acrimonious debate among a small group of animal ecologists (see Connor & Simberloff 1979, 1984; Diamond & Gilpin 1982; Gilpin & Diamond 1982, 1984). Two points are worth making. Ecology as a science has undoubtedly been guilty of too easily embracing competition between animal species as a major force structuring communities, without giving critical thought to how competitive explanations might be distinguished from other explanations. Although we now seem to have cleared this particular hurdle, it turns out that the evolutionary and ecological effects of interspecific competition can be bafflingly (and frustratingly!) difficult to distinguish from random processes (Colwell & Winkler 1984), often requiring field studies of great sophistication (e.g. Schluter & Grant 1984; Schluter, Price & Grant 1985).

The available evidence suggests that the importance of interspecific competition as an assembly rule for animal communities depends very much on the kinds of organisms involved, particularly their size and trophic level, and the nature of their habitat (e.g. Connell 1983; Lawton & Hassell 1984; Schoener 1983; Strong Lawton & Southwood 1984). Unfortunately, none of this information is specifically directed at successional systems; indeed the dearth of studies clearly demonstrating that competitive exclusion is the reason why one animal species replaces another along a terrestrial succession is quite remarkable.

Of course, there are hints of such effects. A number of studies on small mammals show that habitat choice in one or more species is influenced by competitors (see Connell 1983 and Schoener 1983 for reviews), although it is not clear, at least to me, whether the habitats involved are really seral stages. Yapp (1962) suggests that the occasional early appearance in heathland succession of birds more typical of woodland may be due to chance absences of typical heathland bird species, but the data are anecdotal. Spiders provide a possible counter-example. Although spider species show clear and well documented habitat preferences along successional gradients (e.g. Lowrie 1948; van der Aart in Price 1984), there is, as yet, little good evidence for significant interspecific competition among spiders (Wise 1984).

We urgently need studies on animal species in a variety of taxa, specifically designed to test whether interspecific competition is, or is not, a significant cause of species replacements along successional gradients.

Birds on Hawaiian islands

The nearest I can come to a detailed study of competitive exclusion by animals in succession is work by Moulton & Pimm (1983, 1986) on the

introduced avifaunas of six Hawaiian islands. (Exotic birds constitute almost the entire land-avifaunas of these islands below 600m.) Build-up of these exotic bird communities from 1860 onwards is well documented, and yields moderately good evidence for interspecific competition. For example, extinction rates increase as the number of introduced species on each island increases; extinctions are more likely when species have similar sized bills (and hence presumably share similar foods); and some species appear to be kept rare by competitors, even though they are not actually exterminated.

A number of important differences exist between the introduced avifaunas of Hawaiian islands, and a real succession. Rates of arrival and 'discovery' of suitable habitats by birds are certainly different in the two situations, and a significant part of the build-up in avian species richness in real successions can be attributed to changes in the complexity of vegetation (see below) rather than to periodic introductions by man into heavily modified habitats. But if Moulton and Pimm's results have any generality, they suggest that at least part of the turnover of bird species along a succession could be due to interspecific competition, a conclusion that marches in accord with Lack's (1971) views, but for which there is currently no good experimental evidence.

Habitat 'architecture' and animal species richness

Not only do animal species come and go along successional gradients, but as Odum (1969) noted, increased habitat stratification (or vegetation 'architecture') generated by plant succession promotes enhanced animal species diversity. That is, generally more animal species invade the system than disappear as succession proceeds. Again, the phenomenon has a long pedigree, with examples from many taxa (e.g. Lowrie 1948; Duffey 1966; Karr 1968; Healey 1972; Shugart & Hett 1973; Shugart & James 1973; Southwood 1977; Southwood, Brown & Reader 1979; MacMahon 1981; Fuller 1982; Lawton 1983). It constitutes another, simple assembly rule.

Habitat stratification alone, however, is unlikely to be the sole explanation for a general increase in animal species richness during succession, particularly for herbivores. Changes in host-plant diversity must also play a part. The effects of plant species richness, habitat stratification and resource diversity on insect species richness during succession are documented by Southwood, Brown & Reader (1979). (See also Lawton 1983, and Brown & Southwood, Chapter 15 for further discussion.)

Other changes in vegetation

During succession, populations of particular plant species change in density, spatial distribution, patch size, and 'purity', i.e. the extent to which they grow intermingled with other species, (e.g. Yarranton & Morrison 1974). All these properties of vegetation markedly influence the distribution and abundance of phytophagous insects (e.g. Kareiva 1982; Strong, Lawton & Southwood 1984) and must contribute to the turnover of animal species in succession, directly so for phytophages, indirectly for their enemies. With two notable exceptions (Southwood 1977; Southwood Brown & Reader 1983) the problem is ignored in the literature on animal succession; it deserves more attention.

IMPACT OF OTHER ORGANISMS OF PLANT SUCCESSION

Herbivores

Assembly rules for succession become more interesting, and potentially more complicated, when animals are no longer viewed as passive agents responding to changes in vegetation. Herbivores eat plants, and in so doing introduce new rules and alter successional processes (Edwards & Gillman, Chapter 14). Yet one recent review on succession (Finegan 1984) effectively ignores herbivores.

The impact of vertebrate herbivores on the successional dynamics of plant populations has been known for a long time (e.g. Tansley 1935, 1939); more modern reviews are in Crawley (1983), Harper (1977), Jackson (1981), MacMahon (1981), McIntosh (1980) and Whittaker (1953). In marked contrast, the effects of insects on succession have only recently received the attention they deserve although Tansley (1939) guessed that they were important (p. 144), and Costello (1944) provided data on harvester ants. There is now little room to doubt that insect herbivores influence both the rate and the direction of succession, at all seral stages (e.g. Brown 1982, 1985; Brunsting 1982; Brunsting & Heil 1985; Kulman 1971; McBrien, Harmsen & Crowder 1983; Schowalter, Hargrove & Crossley 1986; Tenow 1983). Edwards & Gillman (Chapter 14) and Brown & Southwood (Chapter 15) review the evidence.

Pathogens

Chestnut blight and Dutch elm disease are powerful reminders that plant

population dynamics can be profoundly altered by pathogens. Build-up of plant diseases is one of the reasons why farmers are forced to rotate crops. 'It seems probable that an entirely similar disease accumulation occurs in soil under more natural vegetation ... (and) may need to be taken into account in interpreting successions' (Harper 1977, p. 110). It would be interesting to know how much apparent 'facilitation' (p. 227) is attributable to pathogens. Burdon & Chilvers (1974) suggest that species diversity in maturing eucalyptus associations may be maintained, in part, by pathogenic fungi, whilst poor seedling performance in the vicinity of parent trees may be due to an accumulation of soil pathogens (Connell & Slatyer 1977). The implications for patterns of succession are obvious, and suggest that tracing assembly rules for vegetation requires the active co-operation not only of botanists and zoologists, but also of plant pathologists.

Mutualists

We know even less about the role of mutualists in the assembly of successional communities. Obvious mutualisms of interest to students of succession are:

- lichens;
- plants and mycorrhizal fungi;
- plants and nitrogen-fixing micro-organisms;
- plants and pollinators;
- plants and seed dispersers;
- plants and ant-visitors to extrafloral nectaries;
- herbivorous insects and attendant ants.

For most of these mutualisms, I can find little consistent evidence to support Odum's (1969) generalization that 'internal symbiosis' (i.e. mutualism) is 'undeveloped' in early seral stages, but well developed in mature communities. Indeed, often the reverse is true.

Lichens are among the classical early colonists of bare rock in primary successions, and hence do not appear to be consistent with Odum's views. Data from mycorrhizal fungi are also equivocal (see Cromack (1981) for a review of the biology of mycorrhizas during succession). In some seres, mycorrhizas establish very early, with levels of infection showing no consistent change as succession proceeds (Fig. 11.1; Nicolson 1960) (see also Daft & Nicolson 1973). Tropical successions may conform more closely to Odum's model (Janos 1980), with mycorrhizas effectively absent from pioneer plant communities; facultatively associated with intermediate seres; and forming obligatory associations with mature trees.

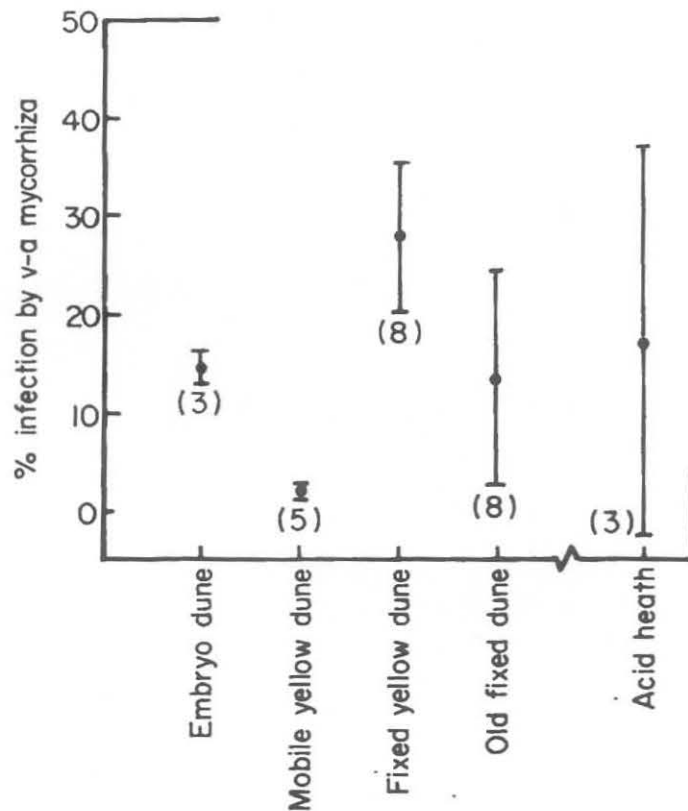


FIG. 11.1. Mean percentage (and 95% CI) of roots of grasses infected with vesicular-arbuscular mycorrhizas in sand dune successions. Data from Nicolson (1960), Tables 1 and 2. Sample sizes in parentheses. The dune successions are at Gibraltar Point, Lincolnshire; Southport, Lancashire and St. Cryus, Kincardineshire. The acid heathland, representative of some late stages of dune succession, is from an inland site at Charnwood Forest. No significant trend exists in the data on percentage infection as succession proceeds, except the low levels of infection in mobile yellow dunes (stage 2), which Nicolson believes to be genuine, and a result of the harsh habitat created by moving sand.

Mycorrhizas infected most species of canopy trees in later stages of succession in Zambia, from open fire degraded chipya woodland to closed evergreen mateshi forest via miombo woodland, although the balance of species changed from predominantly endomycorrhizas to predominantly ectomycorrhizas, or mixtures of both types (Högberg & Pearce 1986). The mycorrhizal status of seres preceding the growth of trees in these areas is apparently unknown. Even less is known about how mycorrhizal infection influences the course and rate of succession. Janos (1980) develops a good circumstantial case for a significant effect on tropical successions (see also p. 239), but experimental data are lacking, and would appear to be very difficult to obtain.

A rather clearer picture emerges from a limited number of studies on plants and symbiotic nitrogen-fixing micro-organisms. Such plants are often conspicuous early colonists of primary successions; for example,

legumes on china-clay works (Marrs *et al.* 1983) and alders on glacial moraines (Crocker & Major 1955). This vital mutualism contributes to a build-up in soil nitrogen and undoubtedly facilitates colonization by plant species characteristic of later successional stages,¹ and hence influences rates, if not patterns of succession (Cromack 1981; Marrs *et al.* 1983; Tilman 1982; Vitousek & Walker, Chapter 10). Such facilitation may be less important in secondary successions, on soils with a greater accumulated capital of organic nitrogen (see Finegan 1984). Data from secondary successions show that chemosynthetic bacteria involved in the nitrogen cycle, namely *Nitrosomonas* (converting ammonia to nitrite) and *Nitrobacter* (converting nitrite to nitrate), are conspicuously more abundant in early seral stages (Rice & Pancholy 1972; Fig. 11.2), and may be virtually absent from climax communities. It seems not to be known how other components of the nitrogen cycle, particularly nitrogen-fixing micro-organisms, change in abundance during secondary succession.

I suspect that a number of other mutualisms may turn out to be very important early in community development, but they have been too poorly studied in this context to be sure. Limited data on mutualistic associations between ants and plants with extrafloral nectaries point to greater ant activity and a higher density of plant species with extrafloral nectaries in early and mid-successional communities, at forest edges and in clearings (Bentley 1976, 1977). The differential protection against herbivory offered by ants to plant species bearing extrafloral nectaries could clearly influence succession.

So too, could ant protection of insect herbivores, particularly Homoptera and butterfly caterpillars in the family Lycaenidae. Ant attendance often (but not always) leads to enhanced herbivore survival, and ultimately to a detrimental impact on selected host-plant species (Strong, Lawton & Southwood 1984). Pierce (1984) shows that a high proportion of ant-attended lycaenid caterpillars exploit legumes as host-plants, perhaps suggesting that this fascinating mutualism is again more frequent in the early stages of succession. (A comprehensive study of the biology and host-plant utilization of all lycaenids for which data are available may soon clarify the frequency of this particular mutualism on plants characteristic of different stages of succession, e.g. annuals and perennials: N.E. Pierce, in prep.)

Finally, the impact of seed dispersers on rates of succession deserves comment. (Seed dispersers undoubtedly benefit plants; the reciprocal benefits are sometimes less certain. Hence, the processes may either be mutualistic or commensal.) Both Finegan (1984) and MacMahon (1981) provide brief reviews. As Edwards & Gillman (Chapter 14) point out,

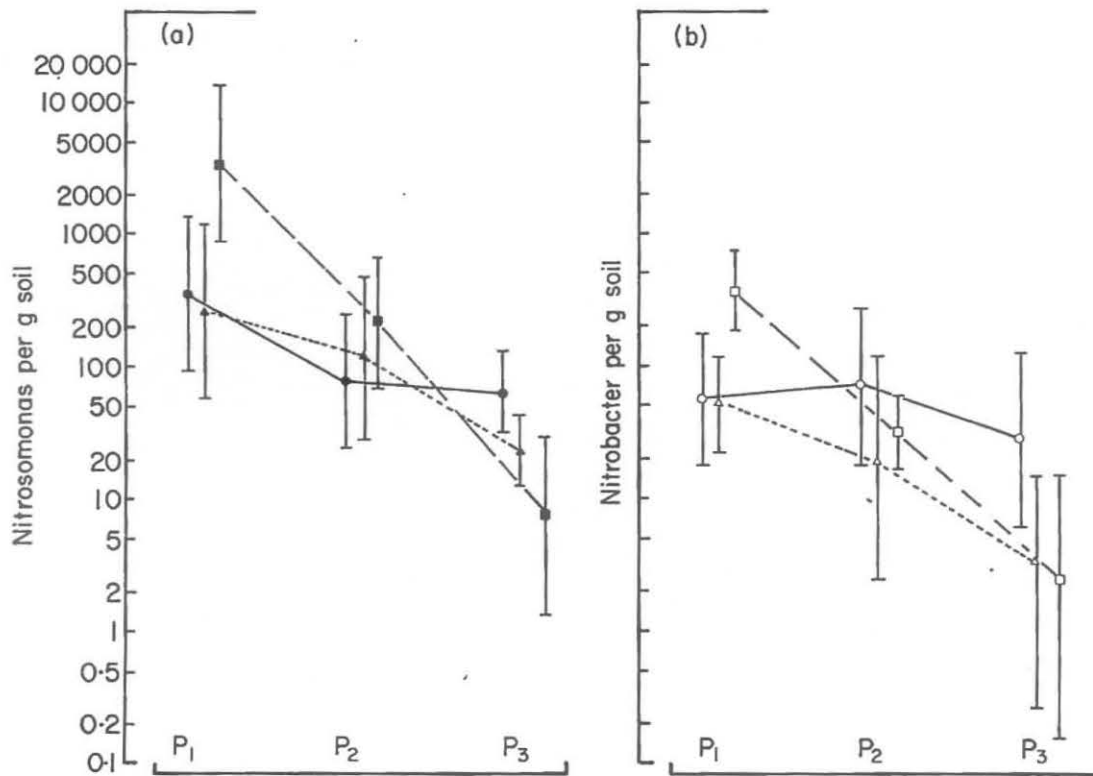


FIG. 11.2. Numbers of micro-organisms g^{-1} soil in three secondary successional sequences (from data in Rice & Pancholy 1972). (a) *Nitrosomonas* (b) *Nitrobacter*. Plotted are means ($\pm 95\%$ CI) of six samples, taken at 2-month intervals between April of one year and February of the next, each sample itself being the mean of four determinations from soil 0–15 cm deep. Data were transformed to $\log_{10}(n + 1)$ before calculating, and back-transformed prior to plotting. Successions are to climax tall grass prairie (circles and solid lines), post oak–blackjack oak (triangles and dotted lines) and oak–pine (squares and broken lines), all commencing in abandoned agricultural fields. P_1 – P_3 are sampling stations as specified by authors: P_1 , 1–2 year old abandoned fields; P_2 , 6-year old prairie succession, 8-year old post-oak succession, 25 year old oak–pine succession; P_3 , climax communities (undated). With one exception, numbers of micro-organisms from this stage in the nitrogen cycle fall during succession.

seed dispersal by animals over short (e.g. by ants) or long (e.g. by birds) distances probably plays a vital part in determining both patterns and rates of succession.

Drawing these arguments together, it is clear that mutualisms are among the most interesting, but also one of the most poorly studied processes contributing to assembly rules for successional communities. Studies to document the frequency and intensity of various mutualistic associations in different seral stages would be valuable. Even more enlightening would be experiments to ‘uncouple’ or disrupt particular mutualisms, and then follow what happens to succession.

WEBS OF INTERACTIONS

Studies on interspecific competition, predation, herbivory and mutualisms ultimately mesh to yield community-wide webs of interactions. A rapidly developing theoretical literature points to some important, and hitherto unexpected, assembly rules that are properties of the entire interactive web (Pimm 1982); once again, pertinent field data from successional systems, useful for testing these ideas, are few.

Attempts to show that the broad trophic structure of developing communities (the proportions of herbivores, detritivores, predators and so on) is somehow constrained by species interactions, and converges to relatively fixed proportions during community development irrespective of the species involved (Heatwole & Levins 1972), are at best equivocal (Simberloff 1976). As with competitive interactions (p. 229) it has proved extremely difficult to distinguish community-wide patterns generated by trophic interactions, from random effects (Cole 1980; Diamond & Gilpin 1982; Van Valen 1982). However, an approximately constant ratio for number of predator species/number of prey species emerges as a clear property of model food-webs, allowed to 'grow' under a process akin to succession (Mithen 1984; Mithen & Lawton 1986; Drake 1985) (Figs. 11.3 and 11.4), and is consistent with some field data (e.g. Jeffries & Lawton 1985). Comparable information on predator: prey and other 'trophic-ratios' (e.g. Brown & Southwood 1983) from successional communities would be valuable.

A number of recent studies have modelled community development by drawing species from a pool of potential colonists (e.g. Pimm 1982; Post 1983; Post & Pimm 1983; Drake 1983; 1985). These studies, and the comparable one by Mithen & Lawton summarized in the previous paragraph, model species interactions using Lotka-Volterra equations (see legend to Fig. 11.3), with all their attendant simplifications and uncertainties. Their results, however, broadly match what we might reasonably expect to happen during succession. For example:

- (a) Species accumulate in the model systems with time, but at steadily decreasing rates. It gets harder and harder for new species to invade the model communities (Post 1983; Post & Pimm 1983; Drake 1985).
- (b) 'Turnover' of species slows down. Species persist in the community for longer, later in the life of the model (Pimm 1982; Drake 1985).

These assembly rules are generated by the whole web of interactions, with community development constrained by levels of connectance,

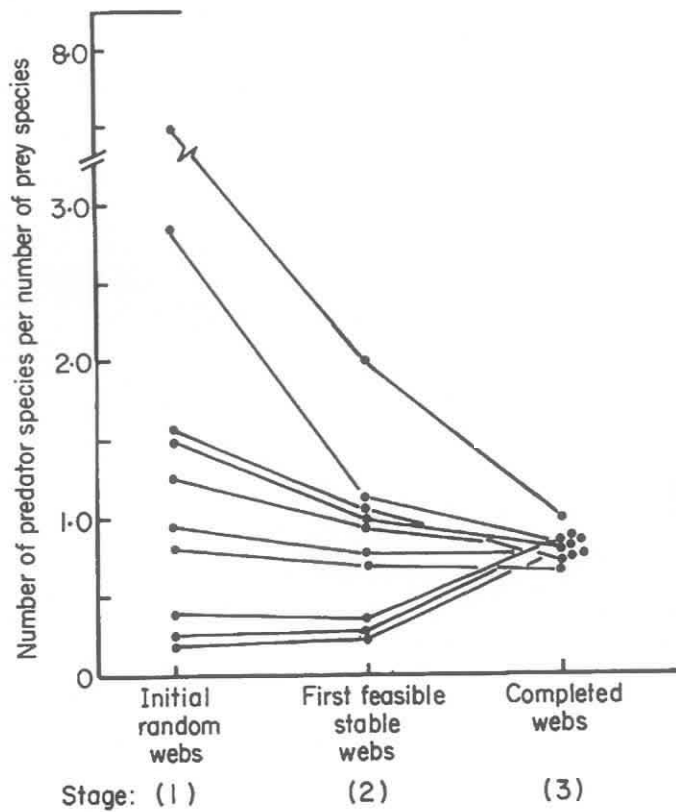


FIG. 11.3. Ratio: Number of predator species/number of prey species in simple two trophic-level Lotka-Volterra models simulating community assembly from a pool of potential colonists (Mithen & Lawton 1986). The ratio varies widely in initial, random draws from the pool (stage 1). The ratio is less variable in the first feasible (i.e. all populations have positive equilibria), stable webs (stage 2). Repeated invasions, extinctions, and species establishment ultimately results in final communities (stage 3) with very tightly constrained ratios. The exact value of this ratio depends on the parameter values used in the model (i.e. upon the 'biology' of the model species making up the web). The model is:

$$\frac{dN_i}{dt} = N_i \left\{ b_i - a_i N_i - \sum_{j=1}^P \alpha_{ij} P_j \right\}$$

$$\frac{dP_j}{dt} = P_j \left\{ -b_j - a_j P_j + \sum_{i=1}^n \alpha_{ji} N_i \right\}$$

where N_i = density of i th prey species ($i = 1 \dots n$); P_j = density of j th predator species ($j = 1 \dots p$); a_i, a_j = intraspecific competition coefficient; b_i = birth rate of i th prey species; b_j = death rate of j th predator species; α_{ij} = effect of j th predator on the i th prey; α_{ji} = effect of i th prey on j th predator. Parameter values were chosen according to the logic in Pimm & Lawton (1977) and Pimm (1982). In this run they were selected at random from the following ranges: b_i (0, 0.1), b_j (-0.1, 0), a_i (-1.0, 0), a_j (-1.0, 10), $|\alpha_{ij}|/|\alpha_{ji}|$ 10, with $\alpha_{ij} \min = \alpha_{ji} \min = 0$, and the constraint that connectance (proportion of α_{ij} s > 0) = 0.4 in the species pool from which colonists were drawn.

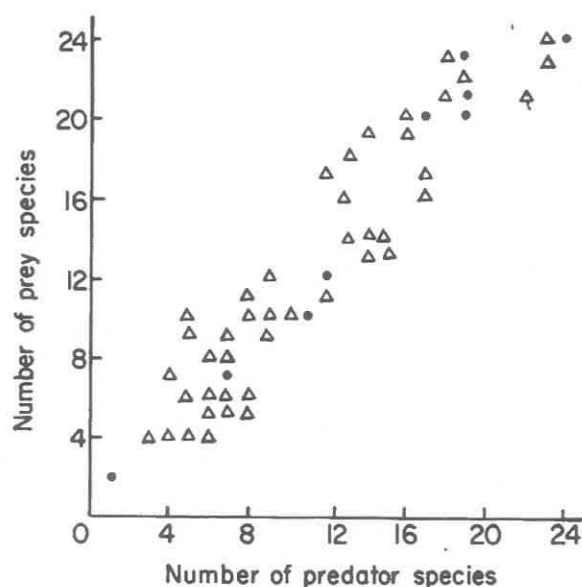


FIG. 11.4. Plot of number of predator species: number of prey species in Lotka-Volterra food-web models, at the end of the community assembly process (stage 3 of Fig. 11.3). Despite a wide range of species occupying the final communities, the ratio of predator to prey species is constrained within narrow limits, in a manner reminiscent of that seen in some field data (e.g. Jeffries & Lawton 1985). The slope of the line (i.e. the predator: prey ratio) depends upon the parameter values in the model (Mithen & Lawton 1986). (Δ single point; \bullet two coincident points).

'apparent competition' and other indirect species interactions, degrees of omnivory, food-chain length and so on (see Holt 1977; Pimm 1982; Pimm & Lawton 1983; Dethier & Duggins 1984; Bender, Case & Gilpin 1984). It is not yet clear how generally these same constraints operate in real successional communities. It is known that the rate of species loss from real communities decreases steadily as succession proceeds (Shugart & Hett 1973; Głowaciński & Järvinen 1975). Unfortunately, these data measure extinction rates in real time, not generation times, and since plants from later successional communities live much longer than primary colonists, I would expect species extinction rates (be they for plants, or the animals that depend on plants) to be slower later in succession. Model species, in contrast, have fixed, arbitrary generation times, making comparisons with extinction rates of real organisms based on generation times (the only sensible comparison) very difficult.

There are also other reasons for interpreting these models very carefully; some at least (e.g. Post & Pimm 1983) fail to mimic the decline in plant species richness observed in many late successional communities,

in studies ranging from Clements (1905) to Southwood, Brown & Reader (1979). Clearly, scope exists to make such models more realistic.

One assembly rule to emerge from these models is startling. Drake (1985) shows that initial random differences in the order in which species colonize the model community can 'lock' the subsequent development of the system into quite different pathways. This means that model 'climax communities' have alternative, relatively *deterministic* end-points dependent upon *random* initial conditions. Moreover, he can reproduce the same 'priority effects' in laboratory microcosms, subject to colonization from a pool of species under his experimental control. Drake is sensibly cautious to point out that his results cannot be applied directly to community assembly in the field. Nevertheless, a growing number of field and laboratory studies show, or are consistent with, similar priority effects (e.g. Talling 1951; Cole 1983; Kneidel 1983; Morin 1984). In the successional literature the idea is hinted at by Whittaker (1953, p. 55) and explicitly developed by Horn (1981) who postulates that initial differences in the abundance of tree species may generate alternative climax forest communities 'dependent upon accidents of history'. Janos (1980) has also suggested that initial differences in soil fungi, particularly whether or not mycorrhizas are present in nutrient-poor tropical soils, may create priority effects that alter the whole course of succession, again culminating in alternative climax communities.

If such priority effects turn out to be common in the field, they will make it doubly difficult to discover whether assembly rules exist from studies based solely on the end-points of community development. Priority effects mean that although there are rules, the way in which they work out in particular circumstances depends upon who got there first, i.e. upon a mixture of initial chance and subsequent determinism.

Unfortunately, the problem is even harder than this, because in order to demonstrate priority effects we must be able to eliminate other explanations for alternative end-points to succession; for example, local differences in habitat management, soil or climate (Tansley 1939; see Sousa & Connell 1985 for a recent discussion). We must also be able to identify the habitat patches (or 'communities') that have developed in different directions, a problem that has proved to be notoriously intractable (see, for example, Whittaker's 1953 exposition on the 'climax pattern hypothesis').

Distinguishing between the effects of chance and determinism on community assembly undoubtedly constitutes one of the most important and difficult problems in contemporary ecology.

ARE THERE ASSEMBLY RULES FOR SUCCESSIONAL COMMUNITIES?

The broad answer to this question is clearly 'yes'; the details are considerably more fuzzy. Assembly rules for successional communities certainly involve more than interspecific competition between plant species, as the range of possible 'pairwise' interactions in Table 11.1 makes plain. Beyond that it is not possible to say which of the many possible species interactions discussed in this chapter generally contribute most to determining patterns and rates of succession; probably all are important some of the time. It is remarkable that a subject with so long a pedigree as community assembly during succession should be so poorly understood, and so lacking in basic data.

ACKNOWLEDGMENTS

A.H. Fitter and B. Hopkins provided help with literature on mycorrhizal fungi and nitrogen-fixing organisms; N.E. Pierce discussed lycaenid-ant mutualisms with me. J.A. Drake kindly allowed me to quote from his unpublished manuscripts. S.L. Pimm provided valuable discussions on 'growing' food-webs, and on effects of community-wide webs of interactions. The following colleagues made helpful and constructive comments on the manuscript: V.K. Brown, M.J. Chadwick, M.J. Crawley, R. Law, M.B. Usher and M.H. Williamson.

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